MADROÑO, Vol. 52, No. 3, pp. 158–165, 2005

INFLUENCE OF PLANT SIZE AND CLIMATIC VARIABILITY ON THE FLORAL BIOLOGY OF *FOUQUIERIA SPLENDENS* (OCOTILLO)

JANICE E. BOWERS
U.S. Geological Survey, 1675 W. Anklam Rd., Tucson, AZ 85745
jebowers@usgs.gov

ABSTRACT

The floral biology of *Fouquieria splendens* (Fouquieriaceae), a drought-deciduous shrub with wandlike branches, was studied in the northern Sonoran Desert. Two different measures of plant size, number of branches long enough to flower (>1 m in length) and actual number of reproductive branches, were used to examine the effect of plant size on reproductive output and floral display. Number of flowers and fruits increased with either measure of plant size. Annual flower production ranged from 190 to 6465 per plant and averaged 2553. Annual fruit production ranged from 9 to 1760 per plant and averaged 390. Because some branches long enough to flower did not do so, number of reproductive branches was a stronger predictor of flower production than number of branches > 1 m long. Inflorescence size (mean number of flowers per panicle) was not significantly related to plant size (number of flowering branches) in 2002 or 2003; in fact, the range in inflorescence size on certain individual plants was about as wide as the range for the entire sample. Interannual variation in floral parameters was examined by monitoring the same set of branches in two years, one unusually dry, one with nearly normal rain. In 2002, the dry year, panicles were numerous and sparsely flowered; in 2003, the wetter year, panicles were relatively few and much more densely flowered. Although flowers *appeared* normally abundant in the wetter year, mean number of flowers per branch was in fact 39% lower than in the dry year. Percent fruit set per panicle in 2003 (36%) was more than twice that in 2002 (16%). Even so, average number of fruits per branch did not differ between 2002 and 2003. Evidently flower production on a per-branch basis was high enough in 2002 to compensate for poor fruit set in that year, resulting in about as many fruits as in 2003.

RESUMEN

La biología de las flores de *Fouquieria splendens* (Fouquieriaceas), un arbusto tolerante de sequía con ramas como varitas, fue estudiada en parte norte del desierto sonorense. Dos medidas diferentes del tamaño de la planta, el numero de ramas suficiente largas para producir flores (> 1 m del largo) y el numero de las ramas en realidad con flores, fueron usadas para examinar el efecto del tamaño de la planta en la producción reproductora y la exposición de las flores. El numero de las flores y las frutas aumentaron con ambas medidas del tamaño de la planta. La producción anual de las flores fue entre 190 y 6465 por planta con un promedio de 2553. La producción anual de las frutas fue entre 9 y 1760 por planta con un promedio de 390. Porque algunas ramas suficiente largas para producir flores no florecieron, el numero de las ramas en realidad con flores fue mejor que el numero de las ramas más largas de un metro para predecir la producción total de flores. El tamaño de la inflorencia (el numero promedio de las flores por panícula) no fue correlacionado significantemente con el tamaño de la planta (como el numero de las ramas con flores) en 2002 o 2003; en realidad, la variedad en el tamaño de la inflorencia en ciertas plantas fue más o menos lo mismo que la de todos de las plantas medidas. La variacíon entre años en los parámetros de las flores fue estudiado por observar el grupo mismo de ramas en dos años, un año muy seco, el otro con lluvia casi normal. En 2002, el año seco, hubo muchas panículas con pocas flores; en 2003, el año con más lluvia, hubo menos panículas pero con muchas más flores por panícula. Aunque las flores parecieron normalmente abundantes en el año con más lluvia, el numero promedio de flores por rama en realidad fue 39% menos que en el año seco. El porcentaje de frutas producidas por panícula en 2003 (36 %) fue más que doble lo del 2002 (16 %). Sin embargo, el numero promedio de frutas por rama fue diferente entre 2002 y 2003. Obviamente la produccíon de flores en la base por rama fue suficiente en 2002 para compensar por la peor produccíon de frutas en ese año, lo que resultar en casi el mismo numero de frutas como en 2003.

Key Words: floral biology, flower production, *Fouquieria splendens,* fruit production, fruit set, interannual variation, Sonoran Desert.

Flower and fruit production integrate a plant's physical and biological environment, serving as an assay of the combined effects of pollinator behavior, climatic variability, and resource limitation. Ecologists use estimates of flower or fruit production in quantifying the floral resources available to pollinators (e.g., Hocking 1968; Tepedino and Stanton 1981); in assessing selective pressures on inflorescence architecture (e.g., Worley et al. 2000; Galloway et al. 2002); and in determining population growth rates and other demographic parameters (e.g., Mandujano et al. 2001). Within species, plant size can have a substantial impact on reproductive output: for the columnar cactus *Carnegiea gigantea*

(Engelm.) Britton & Rose, every additional branch has the potential to augment flower production by about 100 flowers (Steenbergh and Lowe 1977). Plant size can modulate the influence of climatic variability on annual flower production of some woody plants. In a four-year study of *Opuntia engelmannii* Salm-Dyck., for example, the number of flowers initiated by a sample of 26 plants did not vary significantly among years even though winter rain in those years ranged over an order of magnitude (Bowers 1996).

Although plant size is a crucial component of flower production, counting all flowers on large shrubs or trees is scarcely feasible for many species, leaving ecologists with no choice but to subsample, often with little or no regard to variation in plant size (e.g., Solbrig and Cantino 1975; Simpson 1977; Boyd and Brum 1983). In the Sonoran Desert, *Fouquieria splendens* Engelm. (Fouquieriaceae) is probably about as large and fecund a plant as can be conveniently assessed without subsampling. Previous studies of this species have emphasized the effect of pollinators on fruit and seed production (Waser 1979; Scott 1989) while downplaying the effect of climatic variability on flower production (Darrow 1943; Scott 1989), but none have examined the influence of plant size on reproductive output or floral display. The main objective of this study was to determine the effect of plant size on the floral biology of *F. splendens,* including annual flower and fruit production, inflorescence size, and proportion of fertile branches.

A secondary objective of this study was to examine interannual variation in floral display and reproductive output. Several observers have concluded that climatic variability has little influence on flower production in *F. splendens,* but this conclusion depends on subjective impressions (Shreve 1925; Humphrey 1975), which can be misleading, or on counts of inflorescences (Darrow 1943), which are a reliable measure of flower production only if number of flowers per inflorescence is stable from year to year. The only between-year comparison of *F. splendens* flower production (Scott 1989) found significant interannual variation at one of three Chihuahuan Desert sites; somewhat unexpectedly, plants produced more flowers after the drier winter.

In this study, I harvested and counted all flowers, inflorescences, and fruits on 10 plants in two years to determine how flower and fruit production, inflorescence size, and proportion of fertile branches vary with plant size. Because removal of all flowers or fruits could conceivably influence reproductive output in the following year, different plants were sampled in 2002 and 2003. No between-year comparisons were made with these samples. Rather, I monitored inflorescence size, inflorescence number, and fruit set on a sample of branches in an unusually dry year and in a year of nearly normal rainfall to assess the potential for interannual variation in reproductive output. Specific questions addressed were: Does inflorescence size (number of flowers per panicle) vary from year to year and plant to plant? To what extent does plant size determine inflorescence size, inflorescence number, and reproductive output? Does plant size account for variation in the proportion of branches that reproduce each year? Is inflorescence production a reliable guide to flower production? Are flower production and fruit set independent of precipitation in the preceding year?

Methods

Study Area

The study was conducted at Tumamoc Hill (32°13′N, 111°05′W), an outlier of the Tucson Mountains, Pima County, Arizona, USA. The study area, which encompasses about 352 ha, is owned and operated by the University of Arizona as the Desert Laboratory and is situated just west of downtown Tucson, Arizona. The Desert Laboratory grounds include Tumamoc Hill proper, a rocky, basaltic-andesitic knoll (760 to 948 m above sea level), and the level or gently rolling plain to the west (725 to 760 m above sea level). Domestic livestock have been excluded from the study site since 1907. At Tucson, rainfall averages 280 mm per year. Almost half comes during July, August, and September; most of the remainder falls between November and March (Sellers et al. 1985). Average maximum and minimum daily temperatures are 18.6°C and 2.4°C during January, the coldest month, and 37.9°C and 22.8°C in June, the hottest month (Sellers et al. 1985). Vegetation at Tumamoc Hill is typical of the Arizona Upland subdivision of the Sonoran Desert (Shreve 1951). In addition to *F. splendens,* dominant plants include *Cercidium microphyllum* (Torr.) Rose & Johnston, *Carnegiea gigantea, Larrea tridentata* (Sessé & Moç. ex DC.) Cov., *Ambrosia deltoidea* (A. Gray) Payne, *Acacia constricta* Benth., and *Ferocactus wislizeni* (Engelm.) Britton & Rose.

Study Species

Fouquieria splendens is a woody plant with several to 100 wandlike, ascending or erect branches that arise from a very short trunk. The species is locally common in desert scrub and grassland throughout the southwestern United States and northern Mexico (Turner et al. 1995). Branches grow in length when terminal buds elongate during the summer rainy season (Darrow 1943). In a six-year study in the vicinity of Tucson, Arizona, branches < 1 m in length elongated annually but did not flower (Darrow 1943). Mature branches, on the other hand, flowered annually and elongated but every two or three years, if at all (Darrow 1943). Throughout its range, *F. splendens* typically flowers in spring, rarely in autumn (Turner et al. 1995).

Prolonged drought (several years) can suppress flowering entirely (Carlquist 2001). The hermaphroditic, red, tubular flowers are 6 to 22 mm long and are borne in panicles of cymes near the branch tips (Henrickson 1969). Number of panicles per branch increases with branch length (Darrow 1943). Flowers can self pollinate but only to a limited extent (Waser 1979), and the breeding system is best regarded as self-incompatible (Scott 1989). On average, a mature plant annually produces about 2000 flowers (Scott et al. 1993), 200 fruits (Waser 1979), and 800 to 2200 seeds (Waser 1979). The primary pollinators are hummingbirds and carpenter bees (Waser 1979; Scott 1989; Scott et al. 1993). Scott (1989) reported natural fruit set as high as 82% from some Chihuahuan Desert sites and achieved 88% fruit set by outcrossing flowers by hand. He concluded that when pollinators are plentiful, plants have the resources to set large numbers of fruits.

Effect of Plant Size on Reproductive Output and Floral Display

Flower production was determined in April 2002 and April 2003. Different plants were sampled in successive years. In each year, 10 plants were selected to represent a range of sizes, that is, number of branches. Size of each plant was measured in two different ways: as number of potentially reproductive branches (branches > 1 m long) and as number of branches that actually reproduced (flowering branches). All panicles on each plant were removed and placed in labeled paper bags. The number of flower buds and flowers on each panicle was counted and recorded by plant; any unattached flowers in the bottom of the bag were added to the total for the plant.

To examine the influence of plant size on total flower production in each year, number of flowers per plant was used as the dependent variable in separate linear regressions against number of branches > 1 m long and against number of flowering branches. Because total flower production reflects both inflorescence production (number of panicles per plant) and inflorescence size (number of flowers per panicle), either of which might change with plant size, several more analyses were performed. To examine the influence of plant size on inflorescence production, number of panicles per plant in each year was regressed against number of flowering branches per plant. To assess whether plant size affects inflorescence size, the range in inflorescence size in 2002 and 2003 was summarized graphically by showing for each plant the largest and smallest panicles (maximum and minimum number of flowers per panicle) and the mean number of flowers per panicle. In addition, mean number of flowers per panicle was regressed against number of flowering branches per plant. Separate regressions were performed for 2002 and 2003. These analyses used the 10-plant samples described above.

Fruit production was determined in May 2002 and May 2003. Again, 10 different plants in each year were selected to represent a range of sizes, and separate counts were made of fruiting branches and of nonfruiting branches > 1 m long. All fruiting panicles on each plant were harvested, and fruits were counted as for flowers. Number of fruits per plant was plotted as a function of number of branches > 1 m long or number of fruiting branches. In both cases, number of fruits appeared to level off as plant size increased, so nonlinear regression was used to fit a curve to the data points.

There is some between-year variation in number of branches that flower (Darrow 1943). To characterize this variation, the proportion of reproductive branches in each year was calculated for each of the 10 sample plants as number of branches in flower divided by number of branches > 1 long. Linear regression was used to examine the effect of plant size (number of branches > 1 m) on percent of branches that flowered. Proportions were transformed for analysis using the arcsin of the square root.

Interannual Variation in Inflorescence Size, Fruit Set, and Patterns of Abortion

To assess interannual variation in inflorescence size and fruit set, 22 reproductive branches on five plants were tagged and monitored from bud stage in late March to fruit maturation in mid-May in 2002 and 2003. The same branches were monitored in both years. Numbers of flower buds, open flowers, and fruits on individual panicles were counted weekly. Sampling was non-destructive. These data were summarized such that flowering and fruiting effort could be compared between years at each of two levels, panicle and branch. At the panicle level, means for number of flowers initiated per panicle, number of fruits matured per panicle, and proportion of flowers on each panicle that set fruit were calculated for each of the five sample plants. Values for fruit set were transformed for analysis using the arcsin of the square root. Individual plant means were then compared between years using paired *t*-tests; results were reported as grand means across all five plants in 2002 or 2003. At the branch level, means for number of panicles per branch, number of flowers initiated per branch, and number of fruits matured per branch were also calculated for individual plants and compared between years using paired t-tests. Patterns of abortion were examined for three stages (buds, flowers, immature fruits) after summing for all 22 branches the number of structures produced in each stage in each year. Abortion was calculated within stages using the number of structures in a given stage as the denominator and number of structures in the next stage as the numerator. For example, percent of immature

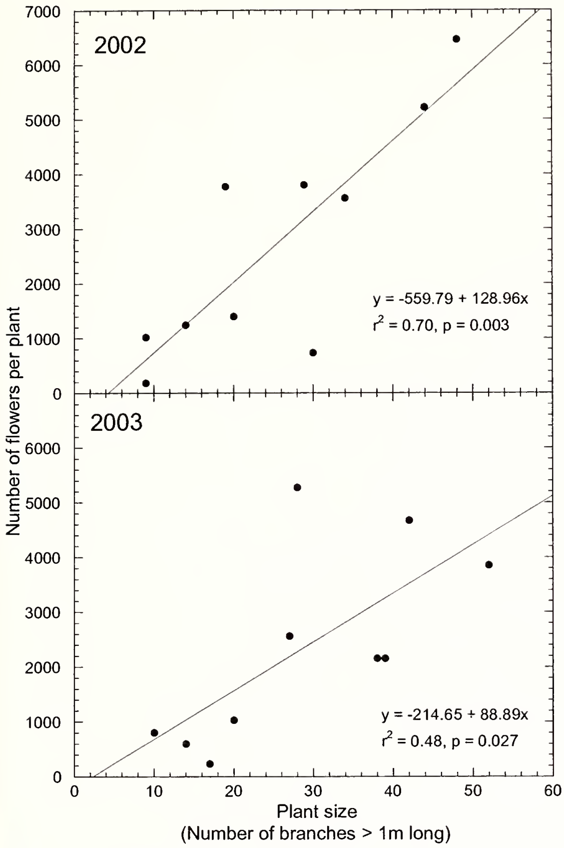

FIG. 1. Relation between plant size, measured as number of branches > 1 m long, and number of flowers in 2002 (top) and 2003 (bottom) for *Fouquieria splendens*, Tumamoc Hill, Tucson, Arizona.

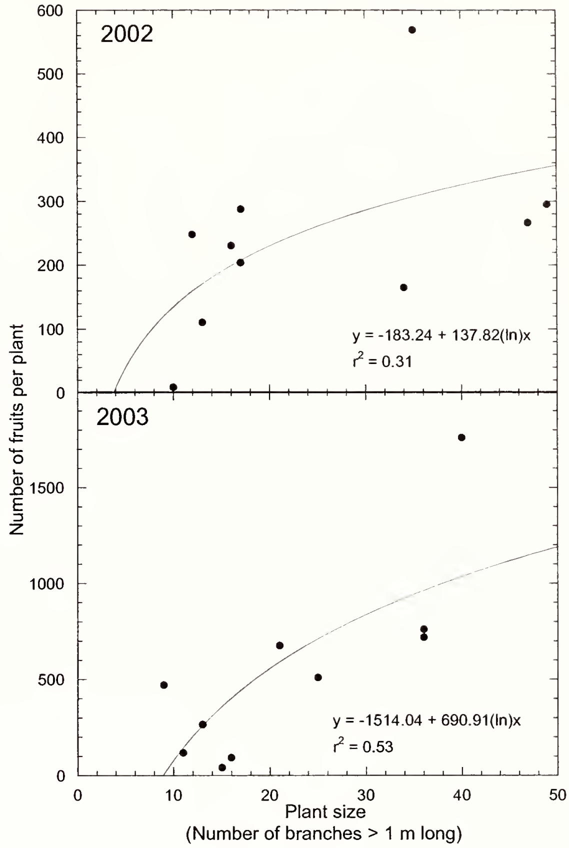

FIG. 2. Relation between plant size, measured as number of branches > 1 m long, and number of fruits in 2002 (top) and 2003 (bottom) for *Fouquieria splendens*, Tumamoc Hill, Tucson, Arizona.

fruits aborted = [1.0 − (number of mature fruits/number of immature fruits)] × 100%. Cumulative abortion was calculated for every stage by summing abortions for that stage and all previous stages, then dividing the total by number of buds.

RESULTS

Effect of Plant Size on Flower and Fruit Production

Flower and fruit production were close to previous estimates (Waser 1979; Scott 1989). When years were pooled (n = 20 plants), there were on average 2553 ± 1942 flowers per plant and 390 ± 394 fruits per plant. (All means are reported as ± 1 SD.) Number of flowers and number of fruits increased with number of branches > 1 m in length. The relation was linear for flowers (Fig. 1) but appeared to be logarithmic for fruits (Fig. 2). The effect of plant size on reproductive output was even stronger when number of flowering or fruiting branches was used as the independent variable. Again, the relation was linear for flowers (Fig. 3), logarithmic for fruits (Fig. 4). Not all branches large enough to flower (>1 m in length) did so: in 2002 and 2003, respectively, the proportion of branches in flower averaged 76% (range = 37% to 100%) and 63% (12% to 80%). The proportion of reproductive branches was independent of plant size (number of branches > 1 m) in both 2002 and 2003 (Fig. 5).

Effect of Plant Size on Inflorescence Production and Inflorescence Size

Inflorescence production (number of panicles per plant) increased linearly with plant size in 2002 and 2003 (Fig. 6). Inflorescence size (number of flowers per panicle), however, appeared to be little affected by plant size. In both years, the range in inflorescence size on certain individual plants was about as wide as the range for the entire 10-plant sample (Fig. 7). In 2002, for example, one plant produced panicles with as few as eight flowers and as many as 182; the range for all 10 plants that year was a minimum of eight and a maximum of 192. The difference between the smallest and largest panicles on a plant typically spanned an order of magnitude (Fig. 7). Inflorescence size (mean number of flow-

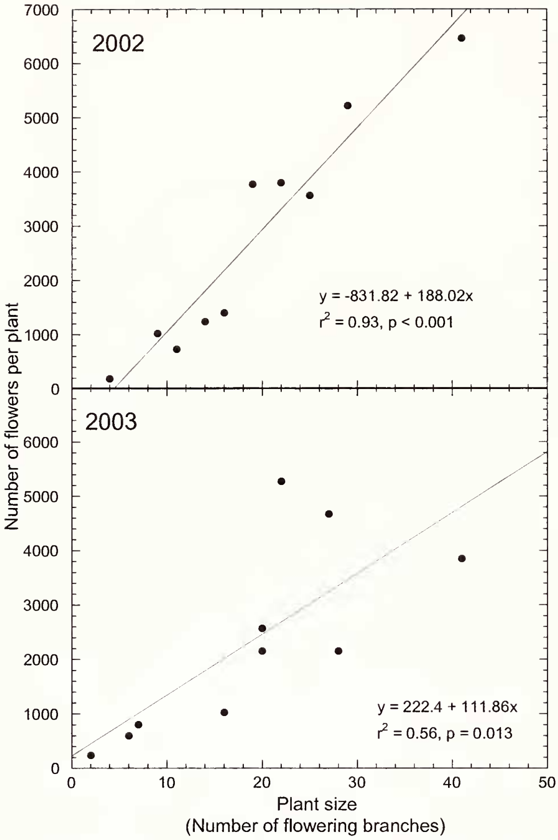

FIG. 3. Relation between plant size, measured as number of flowering branches, and number of flowers in 2002 (top) and 2003 (bottom) for *Fouquieria splendens*, Tumamoc Hill, Tucson, Arizona.

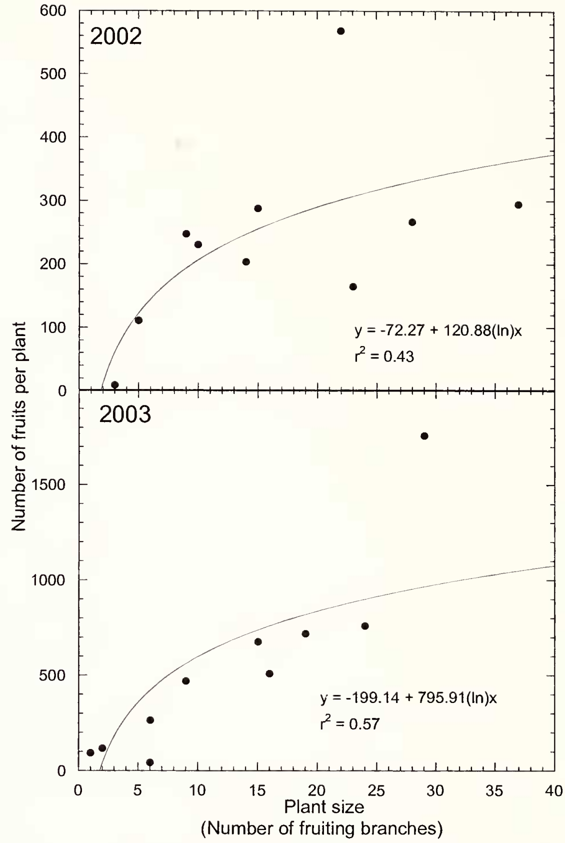

FIG. 4. Relation between plant size, measured as number of fruiting branches, and number of fruits in 2002 (top) and 2003 (bottom) for *Fouquieria splendens*, Tumamoc Hill, Tucson, Arizona.

ers per panicle) was not significantly related to plant size (number of flowering branches) in 2002 ($r^2 = 0.36$, $P = 0.07$) or 2003 ($r^2 = 0.09$, $P = 0.40$).

Interannual Variability in Inflorescence Size, Fruit Set, and Abortion

The 22 tagged branches monitored in two successive years showed marked interannual variability in flower production. The grand mean across five plants was 103 ± 13.0 flowers per branch in 2002 and 63 ± 18.6 flowers per branch in 2003, a significant difference ($t = 5.9$, $P = 0.004$). Reproductive display differed between years as well. Specifically, branches produced many few-flowered panicles in 2002 as opposed to a small number of many-flowered panicles in 2003. The grand mean for number of panicles per branch was 6 ± 1.8 in 2002 and 1 ± 0.3 in 2003, a significant difference ($t = 3.6$, $P = 0.02$). In 2002, five plants averaged 21 ± 6.6 flowers per panicle; in 2003, the average was 59 ± 15.9. Again, means differed significantly between years ($t = 7.2$, $P = 0.002$). Averaged across five plants, fruit set per panicle in 2003 (36% ± 0.1%) was about twice that in 2002 (16% ± 0.1%), but the difference was not significant ($t = 2.5$, $P = 0.07$). Even so, actual number of fruits was significantly lower in 2002 than in 2003 ($t = 5.5$, $P = 0.005$). Specifically, in 2002 the grand mean was 4 ± 2.3 fruits per panicle, whereas in 2003 it was 25 ± 7.5 fruits per panicle. Grand means for number of fruits per branch did not differ between 2002 (19 ± 12.9) and 2003 (26 ± 9.5) ($t = 0.7$, $P = 0.51$).

Patterns of bud, flower, and immature fruit abortion differed somewhat between years on the 22 tagged branches. Table 1 shows percent abortion in each stage (flower bud, flower, immature fruit) and cumulative abortion for the entire flowering season. In 2002, percent abortion was highest in the bud (42%) and immature fruit stages (63%), lowest in the flower stage (22%). In 2003, percent abortion was again highest for buds (50%) whereas approximately equal proportions of flowers (14%) and immature fruits (18%) aborted. Patterns of cumulative abortion were similar between years in the early stages, with 55% and 57% cumulative abortion of buds and flowers in 2002 and 2003, respectively (Table 1). Not until the immature fruit stage was

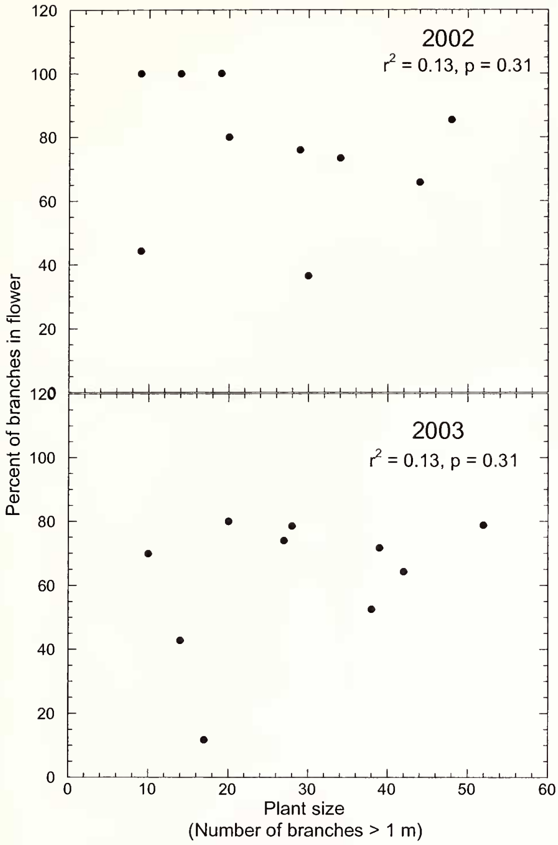

FIG. 5. Relation between plant size, measured as number of branches > 1 m long, and proportion of branches that flowered in 2002 (top) and 2003 (bottom) for *Fouquieria splendens,* Tumamoc Hill, Tucson, Arizona.

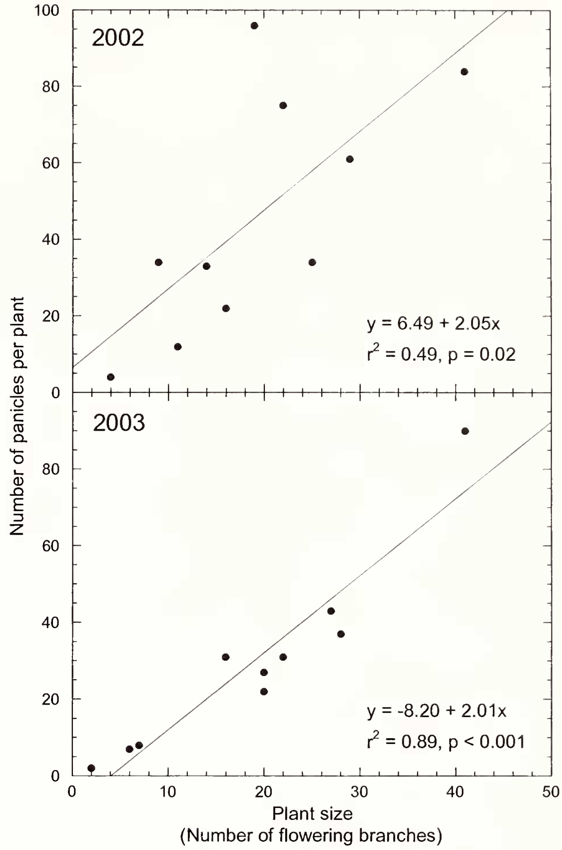

FIG. 6. Relation between plant size, measured as number of flowering branches, and inflorescence production, measured as number of panicles per plant, in 2002 (top) and 2003 (bottom) for *Fouquieria splendens,* Tumamoc Hill, Tucson, Arizona.

there a marked difference between years: the total proportion of structures aborted was 83% in 2002 compared to 65% in 2003 (Table 1).

DISCUSSION

Annual flower production of *Fouquieria splendens* increased linearly with plant size, whether measured as number of potentially reproductive branches (all branches > 1 m in length) (Fig. 1) or as number of branches that actually reproduced (all flowering branches) (Fig. 3). It appeared that the increase in flower production with plant size was a function of more panicles rather than larger panicles (Figs. 6, 7). Although branches > 1 m are large enough to flower, not all do so annually (Darrow 1943); during this study, the proportion of flowering branches per plant ranged from 12% to 100% and averaged 69%. The proportion was independent of plant size (Fig. 5). As for vegetative growth (Darrow 1943), whether a particular branch reproduces in a given year might depend on a complicated combination of seasonal precipitation, branch length, and activity in previous years. Because some branches > 1 m long failed to flower, the number of reproductive branches was a stronger predictor of flower production than number of branches > 1 m long.

There was considerable variation among plants in maximum and mean number of flowers per panicle (Fig. 7), but the variation could not be ascribed to plant size, probably because variation among branches on a single plant overwhelmed any differences between plants. Specifically, long branches produce more inflorescences (Darrow 1943) and larger inflorescences (Bowers, unpublished data) than short branches. Except for very small and very large individuals, most plants have both short and long branches, thus both small and large panicles. Because panicles of all sizes can be found on most plants, there is no relation between plant size and inflorescence size. Insofar as panicle size and number vary with branch length, annual flower production should be more strongly related to the sum of individual branch lengths than to number of branches in flower. However, the difficulty of measuring thorny branches up to 5 m in length makes number of branches a useful proxy.

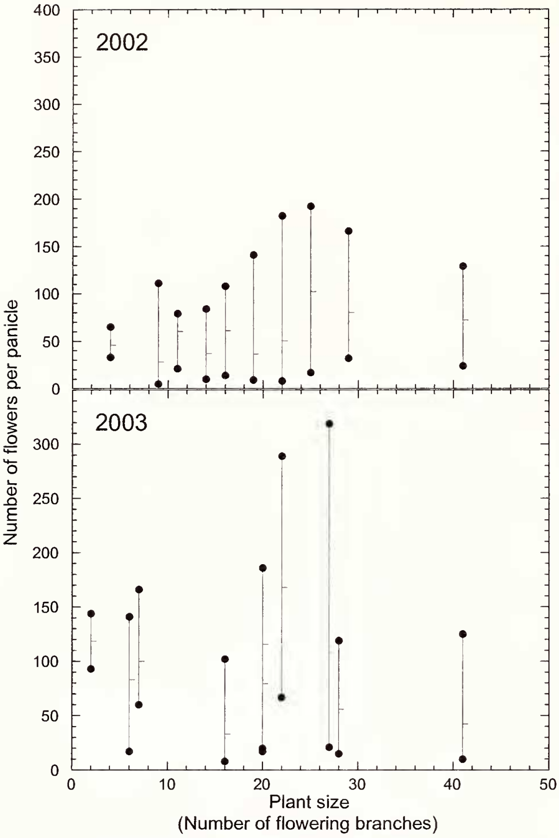

FIG. 7. Between-plant variation in inflorescence size in 2002 (top) and 2003 (bottom) for *Fouquieria splendens*, Tumamoc Hill, Tucson, Arizona. Circles show largest and smallest panicles on each plant (maximum and minimum number of flowers per panicle). Ticks show mean number of flowers per panicle. *X* axis shows plant size, measured as number of flowering branches.

Fruit production, like flower production, increased with plant size and ranged from 9 to 1760 fruits per plant per year (Figs. 2, 4). The relation between plant size and number of fruits was logarithmic, indicating that plants of moderate to large size tended to abort a higher proportion of flowers than small plants. Higher levels of abortion on large plants might reflect increasing inefficiency of pollen transfer as pollinators move among the many inflorescences on a large plant. Pollen is clearly not the only factor that limits fruit production, however; 42% to 50% of abortions took place during the bud stage (Table 1). Resources available to a plant for a given flowering episode might limit the number of buds that develop into flowers; if the effect becomes stronger as plants increase in size, large plants might set no more fruits than moderate-sized plants. Conceivably, both resources and pollen limit fruit production as plants grow (e.g., Campbell and Halama 1993).

Darrow (1943) used number of inflorescences per plant as a measure of flower production in *F. splendens.* Although it is easier to count inflorescences than individual flowers, inflorescence counts can be misleading when comparing flower production among years. Close monitoring of the same set of 22 branches showed that floral parameters differed significantly in two consecutive years. In 2002, panicles were numerous and sparsely flowered; in 2003, panicles were relatively few and much more densely flowered. Although flowers *appeared* normally abundant in 2003, mean number of flowers per branch was in fact 39% lower than in the previous year.

A two-year study is not long enough to determine how reproductive output varies with precipitation, but because of marked differences in seasonal rain between the two years, it is tempting to draw some tentative conclusions. Before the 2002 flowering season, winter-spring (November to April) rain was just 26.2 mm. The 2003 flowering season followed a winter-spring of nearly normal rainfall, 68.1 mm. Number of flowers per branch was 103 in 2002, 63 in 2003. Thus, a 2-fold increase in flower production was accompanied by a 3-fold decrease in rain. In 1987 and 1988, Scott (1989) similarly found a 2-fold increase in flowers per plant with a 4-fold decrease in winter-spring rain. Although the difference between years in rain was relatively large in both studies, the difference between years in number of flowers was relatively modest. It is worth noting that the winter-spring of 2001–2002 was the driest on record at the study site, and several woody species failed to bloom in spring 2002, among them a shrubby tree (*Cercidium microphyllum*), a small shrub (*Ambrosia deltoidea*), and a cactus (*Opuntia engelmannii*) (pers.

TABLE 1. PATTERNS OF *FOUQUIERIA SPLENDENS* BUD, FLOWER, AND FRUIT ABORTION ON 22 BRANCHES IN TWO YEARS AT TUMAMOC HILL, TUCSON, ARIZONA.

	2002			2003		
	Number produced	Percent aborted: Stage	Percent aborted: Cumulative	Number produced	Percent aborted: Stage	Percent aborted: Cumulative
Buds	2264	42	42	1623	50	50
Flowers	1319	22	55	817	14	57
Immature fruits	1025	63	83	700	18	65
Mature fruits	382	—	—	572	—	—

obsv.). Remarkably, *F. splendens* not only bloomed in 2002 but apparently bloomed heavily. Either flower production in this species is not greatly influenced by rain (Shreve 1925; Darrow 1943; Humphrey 1975; Scott 1989), or some other measure of precipitation is more pertinent.

In contrast to flower production, percent fruit set was markedly higher in 2003, after the wetter year. The high level of abortion in 2002 (63% of immature fruits) might have been a consequence of winter-spring drought, although poor pollination and excessive predation cannot be ruled out as contributing factors. Whatever the reason for poorer fruit set in 2002, overall fruit production did not differ between years, apparently because higher flower production in 2002 compensated for lower fruit set.

The floral biology of *F. splendens* reflects the influence of plant size at several points. As plants grow in size, they produce more inflorescences (Fig. 6), thus augmenting annual flower production (Figs. 1, 3). Larger plant size does not necessarily translate into higher fruit production, however; pollinators might become less efficient outcrossers as they move among the many inflorescences on a large plant, and large plants might experience higher levels of resource limitation than small plants. Interannual variation in number of flowers per branch exists but is not large; the main constraint on annual flower production is likely plant size, particularly the number and length of branches that are reproductively active.

Acknowledgments

Thanks to John Hunter, Margrit McIntosh, Steven McLaughlin, and Nickolas Waser for many helpful comments on various drafts of the manuscript.

Literature Cited

Bowers, J. E. 1996. More flowers or new cladodes? Environmental correlates and biological consequences of sexual reproduction in a Sonoran Desert prickly pear cactus, *Opuntia engelmannii*. Bulletin of the Torrey Botanical Club 123:34–40.

Boyd, R. S. and G. D. Brum. 1983. Predispersal reproductive attrition in a Mojave Desert population of *Larrea tridentata* (Zygophyllaceae). American Midland Naturalist 110:14–23.

Campbell, D. R. and K. J. Halama. 1993. Resource and pollen limitations to lifetime seed production in a natural plant population. Ecology 74:1043–1051.

Carlquist, S. 2001. Wood anatomy of Fouquieriaceae in relation to habit, ecology, and systematics: nature of meristems in wood and bark. Aliso 19:137–163.

Darrow, R. A. 1943. Vegetative and floral growth of *Fouquieria splendens*. Ecology 24:310–322.

Galloway, L. F., T. Cirigliano, and K. Gremski. 2002. The contribution of display size and dichogamy to potential geitonogamy in *Campanula americana*. International Journal of Plant Science 163:133–139.

Henrickson, J. 1969. Anatomy of periderm and cortex of Fouquieriaceae. Aliso 7:97–126.

Hocking, B. 1968. Insect-flower associations in the high Arctic with special reference to nectar. Oikos 19:359–388.

Humphrey, R. R. 1975. Phenology of selected Sonoran Desert plants at Punta Cirio, Sonora, Mexico. Journal of the Arizona Academy of Science 10:50–67.

Mandujano, M. C., C. Montaña, M. Franco, J. Golubov, and A. Flores-Martínez. 2001. Integration of demographic annual variability in a clonal desert cactus. Ecology 82:344–359.

Scott, P. E. 1989. Ecological consequences of variation in pollinator availability: ocotillo, carpenter bees, and hummingbirds in two deserts. Ph.D. dissertation. Louisiana State University, Baton Rouge, LA.

———, S. L. Buchmann, and M. K. O'Rourke. 1993. Evidence for mutualism between a flower-piercing carpenter bee and ocotillo: use of pollen and nectar by nesting bees. Ecological Entomology 18:234–240.

Sellers W. D., R. H. Hill, and M. Sanderson-Rae. 1985. Arizona climate. University of Arizona, Tucson, AZ.

Shreve, F. 1925. An unusually arid season in southern Arizona. Pp. 164–165 *in* Carnegie Yearbook, Vol. 24. Carnegie Institution of Washington, Washington, D.C.

———. 1951. Vegetation of the Sonoran Desert. Carnegie Institution of Washington Publication no. 591. Carnegie Institution of Washington, Washington, D. C.

Simpson, B. B. 1977. Breeding systems of dominant perennial plants of two disjunct warm desert ecosystems. Oecologia 27:203–226.

Solbrig, O. T. and P. D. Cantino. 1975. Reproductive adaptations in *Prosopis* (Leguminosae, Mimosoideae). Journal of the Arnold Arboretum 56:185–210.

Steenbergh, W. F. and C. H. Lowe. 1977. Ecology of the saguaro: II. Reproduction, germination, establishment, growth, and survival of the young plant. National Park Service Scientific Monograph Series no. 8. Government Printing Office, Washington, D.C.

Tepedino, V. J. and N. L. Stanton. 1981. Diversity and competition in bee-plant communities on short-grass prairie. Oikos 36:35–44.

Turner, R. M., J. E. Bowers, and T. L. Burgess. 1995. Sonoran Desert plants: an ecological atlas. University of Arizona Press, Tucson, AZ.

Waser, N. M. 1979. Pollinator availability as a determinant of flowering time in ocotillo (*Fouquieria splendens*). Oecologia 39:107–121.

Worley, A. C., A. M. Baker, J. D. Thompson, and S. C. H. Barrett. 2000. Floral display in *Narcissus*: variation in flower size and number at the species, population, and individual levels. International Journal of Plant Science 161:69–79.